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Interspecific variation in growth responses to tree size, competition and climate of western Canadian boreal mixed forests

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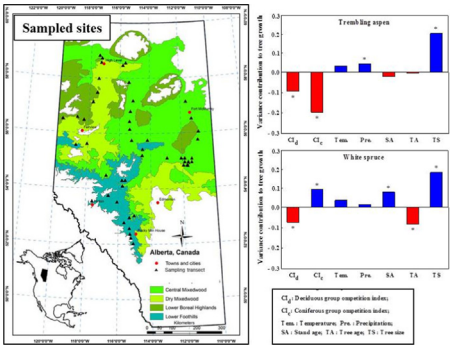
HIGHLIGHTS

- Competition and tree size were two important factors controlling tree growth.
- Effect of climatic indices on tree growth was less important than that of competition.
- Effect of mutualism on tree growth offset that of competition within coniferous group.
- Decline of stem density under drought released competition stress of survival trees.

GRAPHICAL ABSTRACT



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ABSTRACT

Tree growth of boreal forest plays an important role on global carbon (C) cycle, while tree growth in the western Canadian boreal mixed forests has been predicted to be negatively affected by regional drought. Individual tree growth can be controlled by many factors, such as competition, climate, tree size and age. However, information about contributions of different factors to tree growth is still limited in this region. In order to address this uncertainty, tree rings of two dominant tree species, trembling aspen (*Populus tremuloides Michx.*) and white spruce (*Picea glauca* (*Moench.*) *Voss*), were sampled from boreal mixed forest stands distributed across Alberta, Canada. Tree growth rates over different time intervals (10 years interval, 1998–2007; 20 years interval, 1988–2007; 30 years interval, 1978–2007) were calculated to study the effects of different factors (tree size, competition, climate, and age) on tree growth. Results indicated that tree growth of two species were both primarily affected by competition or tree size, while climatic indices showed less effects on tree growth. Growth of trembling aspen was significantly affected by inter- and intraspecific competition, while growth of white spruce was primarily influenced by tree size, followed by competition. Positive relationship was found between growth of white spruce and competition index of coniferous group, suggesting an intraspecific mutualism mechanism within coniferous group. Our results further suggested that competition driven succession was the primary process of forest composition shift in the western Canadian boreal mixed forest. Although drought stress increased

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tree mortality, decline of stem density under climate change released competition stress of surviving trees, which in turn sustained growth of surviving trees. Therefore, climatic indices showed fewer effects on growth of dominant tree species compared to other factors in our study.

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1. Introduction

Variations of forest function, composition, and biomass caused by climate change are expected to feed back on the climate system (Bonan, 2008), while forests play a key role in land-atmosphere exchange processes (Carpenter et al., 2009). Forest tree growth and forest development can be significantly affected by biotic or abiotic factors, such as climate, fire event, competition or insect outbreak (Farrior et al., 2015; van der Sleen et al., 2015). Hogg et al. (2017) reported that climate change could explain about 40% tree biomass increment in pure stands of western Canada. A previous study using tree ring chronologies (remove the competition, age, and size-related variances) of Canadian mixed wood forests reported that climatic variables only captured ~40% variance in tree growth (Jiang et al., 2016), suggesting that there were other important factors influencing tree growth. Variation in forest tree growth may cause significant effect on global C cycle; therefore, it is necessary to quantify the effects of different factors on tree growth in predicting forest development. Forests dynamics and tree growth have been presumed to be driven by climate change on the regional or global scales (Feeley et al., 2007; van Mantgem et al., 2009; Peng et al., 2011). A recent study has also reported that the sensitivity of North American forest to climate will imply large changes in the 21st century (Charney et al., 2016). However, little attention has been paid to the potential effect of competition, while the importance of competition effect is not negligible in determining tree growth (Glenn-Lewin et al., 1992; Silvertown and Charlesworth, 2009). It had demonstrated that competition can directly or indirectly influence tree growth by modifying the growth response to climate change (Clark et al., 2014; Rollinson et al., 2016). Competition and climatic indices interactively affect tree growth, while these effects may vary with tree age, size, species, and stand properties.

Response of tree growth to climate change can be affected by tree size and age (Bennett et al., 2015; Chen et al., 2016). Rate of tree biomass accumulation generally increased with tree size based on the analysis of a global dataset (Stephenson et al., 2014). Growth of old and young trees respond differently or consistently to climate changes, depending on tree species (Jackson et al., 2009). Foster et al. (2016) even reported that effects of size and age on tree growth were more significant than those of climatic variables. On the other hand, it has also been reported that the sensitivity of a target tree to neighbor competition is strongly depending on tree size (Matsushita et al., 2015). Growth of larger trees tend to be greater than that of smaller trees when competition is low, but significantly decreases at a steeper rate with increasing competition (Anning and McCarthy, 2013).

Effects of climate change and competition on tree growth were also dependent on tree species, because different species do not uniformly respond to climate change and competition due to their inconsistent life histories and physiological traits (Messaoud and Chen, 2011; Martinez-Vilalta et al., 2012). Previous studies reported that different tree species responded inconsistent to drought (Colenutt and Luckman, 1995; Yu et al., 2008; Rozas et al., 2009). Luo and Chen (2011) reported that effects of competition and age on tree mortality were different between shade-tolerant and shade-intolerant species. Shade-intolerant species were more sensitive to climate change and neighbor competition than shade-tolerant species (Poorter et al., 2010; Huang et al., 2013), because shade-tolerant species were commonly lower in respiration rates and could create higher wood densities when competition stress was high (Niinemets and Valladares, 2006). Early-successional and late-successional tree species also show different responses to climate and competition. Rollinson et al. (2016) reported that early-successional species commonly showed intense competitive pressure on neighboring stems, and correspondingly depressed the growth of late-successional species, suggesting that interspecific competition would also significantly affect forest tree growth and succession. Therefore, it is necessary to study the effects of climate and competition on growth of different tree species, which is helpful for prediction of forest succession and development.

Boreal forests strongly affect the global C cycle and regional climatology (Bonan, 2008; Ma et al., 2012), which has been considered as a potential tipping component in earth system (Lenton et al., 2008). Recent climate changes, especially extreme drought event, showed substantial impacts on the tree growth, mortality and forest succession in this region (Searle and Chen, 2016). Meanwhile, the effects of drought on tree growth and forest mortality were found to be spatially different (Michaelian et al., 2011; Jiang et al., 2016). Increase in tree mortality significantly threatens sustainable development of boreal mixed forest, but decline in stem number may also correspondingly release stand level competition stress for surviving trees. Therefore, it is necessary to study effects of different factors on tree growth in boreal mixed forest of western Canada.

In this study, we aim to investigate effects of competition, climate, stand age, and stem size on tree growth of dominant species in the western Canadian boreal mixed forests. Towards this goal, tree ring samples of trembling aspen and white spruce were collected from different boreal mixed forest stands in Alberta, western Canada. Based on dendrochronology method, tree growth rates over different time intervals were calculated to 1) examine and compare effects of different factors on tree growth in western Canadian forests, and 2) determine whether responses of tree growth to these factors varied with tree species. It is hypothesized that competition may show more significant effect on tree growth compared to other factors, and effects of competition and climatic indices on tree growth may vary with tree species.

2. Materials and methods

2.1. Study area

The study area includes major boreal mixed forest in Alberta, western Canada (110°W~120°W, 52°N~59°N), which occupy 75% of the forested area of the province (Fig. 1). Our sampled sites distributed from Rocky Mountain House in the south to High Level in the north and from Fort McMurray in the east to Fairview and Hinton in the west. Elevations of the sampled sites ranged from 266 m to 1308 m, while the tree line elevations of the whole study area ranged from 1600 to 2200 m. Dominant tree species in the boreal mixed forests are trembling aspen (*Populus tremuloides Michx.*) and white spruce (*Picea glauca* (*Moench.*) *Voss*) (Stadt et al., 2007). Trembling aspen commonly establish earlier (canopy and shade-intolerant), and white spruces (understory and shade-tolerant) establish later (Chen and Popadiouk, 2002). It was found that white spruce suffered intense competition from pioneer species (Chen and Popadiouk, 2002; Bokalo et al., 2007), and growth of white spruce was significantly influenced by competition of trembling aspen in mixed forests (Cortini et al., 2012). In this region, forested area can be classified as four sub-regions, dry mixedwood, central mixedwood, lower foothills, and lower boreal highlands. This classification is established based on analysis of soil properties, site conditions, vegetation, climate variables, and forest productivity (Beckingham et al., 1996). The study area is primarily affected by cool

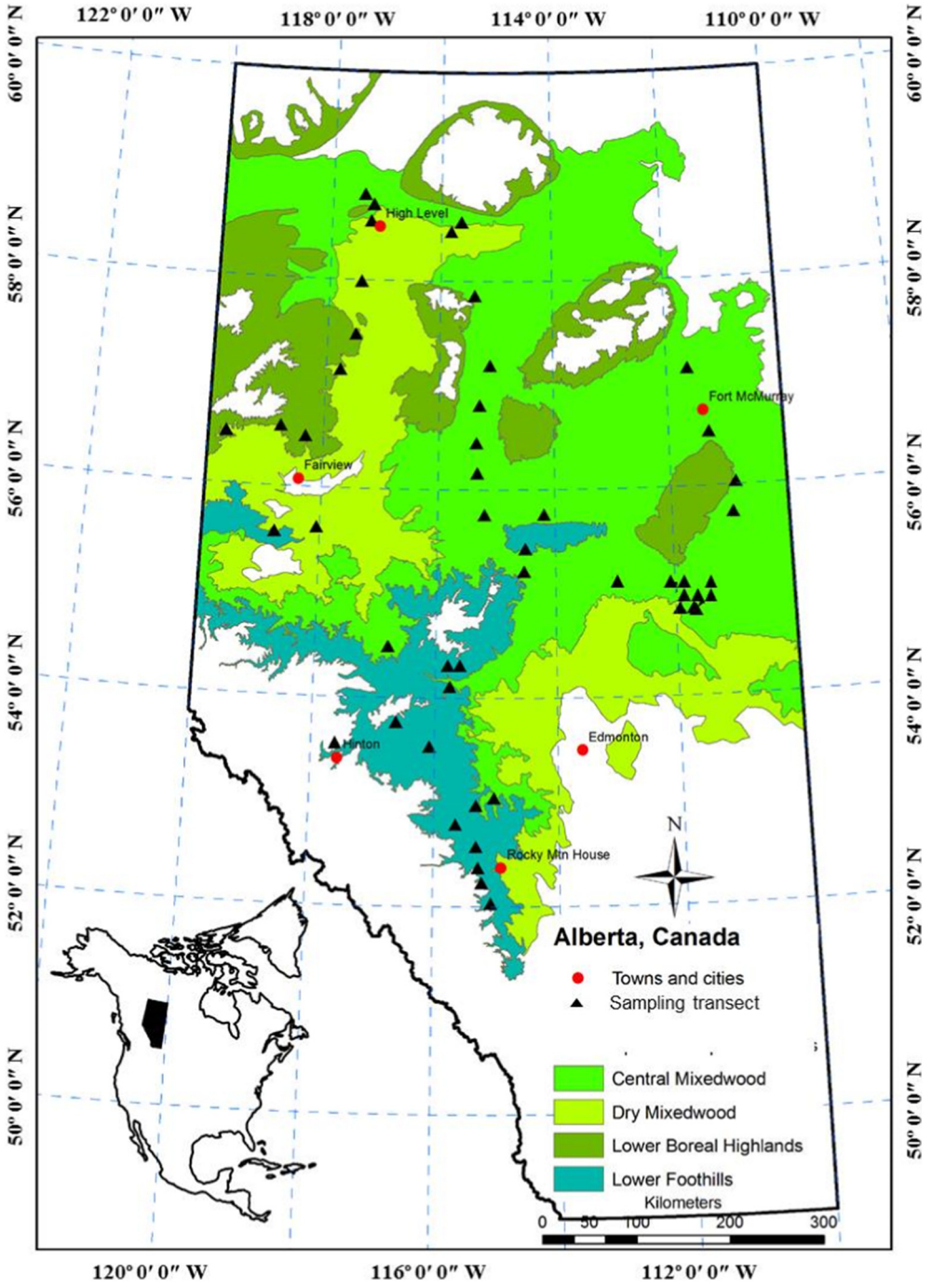

Fig. 1. Map showing the locations of sampling sites in relation to the natural ecoregions of Alberta, Canada. Different colours represent the natural sub-regions, including central mixedwood (green), dry mixedwood (yellow), lower boreal highlands (olive), and lower foothills (light blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and moist Pacific air, but is also influenced by dry continental polar air masses in the winter. In this region, mean annual temperature decreases from south to north. Mean annual temperature and growing degree-days are around 1.0 °C and 1306 °C, respectively. Annual total precipitation increases from northeast to southwest (Huang et al., 2013), and mean annual precipitation of the whole study area is 479 mm with 25–34% in the form of snow (Huang et al., 2013). Sporadic permafrost occurred in the northern Alberta and in mountain area, while our sampling sites were not included in permafrost area. Significant warming and drought were found in this region from 1960 to 2017 (Fig. 2). Based on model scenarios of future climate change, substantial warming and drought stress can be expected over the next century in this area (Price et al., 2013; Wang et al., 2014).

2.2. Climatic data

In this study, mean annual temperature (T), maximum temperature (T_{max}), minimum temperature (T_{min}), precipitation (P), growing degree day (GDD), and climate moisture index (CMI) were derived from BIOSIM software (https://cfs.nrcan.gc.ca/projects/133) (Reginere et al., 2012), which generated historical scale-free annually climate data for specific locations based on latitude, longitude and elevation. Climate and competition may show inconsistent effects on short-term and

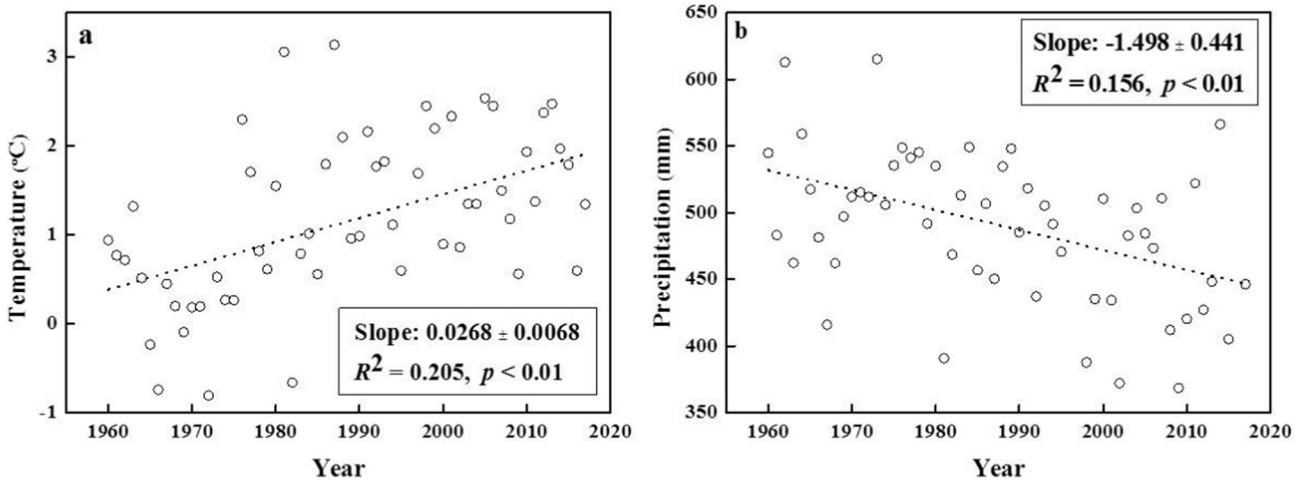

Fig. 2. Temporal trends of a) annual mean temperature and b) annual total precipitation from 1960 to 2017 in Alberta, Canada. The dot line was fitted trends using linear model with slope, R^2, and p values.

long-term tree growth; therefore, tree growth rates and climatic data of different time intervals (10 years interval, 1998–2007; 20 years interval, 1988–2007; 30 years interval, 1978–2007) were calculated in our study. The climatic variables of different time intervals were calculated as the average of climate values over different time intervals. To minimize multicollinearity, pair-wised correlations were analyzed among the different climate variables. Based on the correlation analysis, two variables (T and P) were eventually retained in our study.

2.3. Tree ring data

Tree ring samples were all collected within the study area of western Canada in 2007, 2008, 2010 and 2011. Within the study area, different boreal mixed forest stands (trembling aspen and white spruce dominated) were randomly selected in four natural sub-regions according to the Phase 3 forest inventory database (AESRD, 2012). Stands with indications of ground fires or insect outbreaks were excluded. In each selected stand, a belt transect (average area was 415 m^2) was employed in the center of the distribution area to select subject trees. Stands with low stem density require larger area of transect to obtain sufficient samples. Stem density was measured within each transect. Stand age for each transect was determined using the trembling aspen stump height ring count according to the method of (Huang et al., 2013), while stand age was used to represent the age of sampled forest stand since forest estimation. Within each transect, 8 to 10 live trembling aspens and 8 to 15 live white spruces were randomly chosen as subject trees, and the number of subject trees was depending on transect area. For each subject tree, tree height and diameter at breast height (DBH) was measured. All subject trees were felled using an electric saw, and one disk was cut down at stump height (0.3 m) for each subject tree. The diameter at stump height was measured on sampled discs for each subject tree, and tree ages of all discs were also determined simultaneously (Denneler et al., 2008), while tree age was used to represent the age of each sampled subject tree. In total, 49 transects were assessed and sampled throughout the boreal mixed forests of Alberta, western Canada. We totally selected 426 trembling aspens and 512 white spruces as subject trees.

All tree discs were dried and carefully polished with successively fine grits of sandpaper in the laboratory. Two radii, separated by an angle of 90–180° (avoiding knots or severe reaction wood) were chosen from each disc. Visual cross-dating of each radius was conducted using a binocular microscope. A measuring system with the "Times Series Analysis Program" (Frank Rinntech, Germany) was used to measure the ring width along the dated radii at the precision level of 0.001 mm. After that, visual cross-dating was verified using COFECHA (Holmes, 1983). The correlation between individual series and the master chronology within each transect was above 0.55 ($p < 0.01$), indicating strong similarities in inter-annual ring growth pattern among trees within transects. Chronologies between nearby transects were also well correlated ($r > 0.48$, $p < 0.01$), which suggested that results from cross-dating were reliable. For a given tree, ring-width measurements corresponding to the same year were averaged to represent annual ring growth. After that, basal area increments (BAI, cm^2) of each subject tree over different time intervals (10 years interval, 1998–2007; 20 years interval, 1988–2007; 30 years interval, 1978–2007) were calculated according to the following equation:

$$BAI = \pi\left(R_O^2 - R_I^2\right) \quad (1)$$

where BAI represents basal area increments of each tree over different time intervals; R_O and R_I respectively represents the outermost and innermost radii of tree ring over different time intervals. Finally, tree growth rates (cm^2 $year^{-1}$) were calculated through dividing BAI by time interval.

2.4. Competition indices

For competition assessment, the DBH of all trees (taller than 1.3 m and within a 10 m^2 circle plot centered at each subject tree) were measured within each transect. Competition assessment of each subject tree within one transect was then aggregated to obtain a transect-level assessment of competition during competition indices calculation. Firstly, we calculated three simple competition indices for each subject tree: density (N, stems ha^{-1}), the sum of stem diameter at breast height (SDBH, m ha^{-1}), and the sum of stem basal area (BA, m^2 ha^{-1}). We also evaluated the other three competition indices considering trees thicker than subject trees, denoted as NGR, SDBHGR, and BAGR. Another common competition index, stand density index (SDI) was also calculated and used for statistical analysis. These competition indices have been found to be effective in quantifying the growth-competition relationship (Lilieholm et al., 1993; Filipescu and Comeau, 2007; Stadt et al., 2007). Competition indices were calculated for both deciduous and coniferous groups.

2.5. Data analysis

In our study, linear mixed-effects model (LMM) was used to analyze the relationships between tree growth rates (cm^2 $year^{-1}$) and possible drivers (competition, climate, stand age, and tree size) for different time

intervals (10 years interval, 1998–2007; 20 years interval, 1988–2007; 30 years interval, 1978–2007). Preliminary analysis showed that temperature and precipitation would be better climatic indices compared to CMI; therefore, CMI was excluded in the linear mixed-effects model. The model was as follow:

$$G \sim CI_c + CI_d + T + P + Size + A + SA + \varepsilon \quad (2)$$

where G was tree growth rates; CI_c represents the competition index of coniferous group; CI_d represents the competition index of deciduous group; T and P represent annual temperature and precipitation, respectively; we used DBH as *Size* of subject tree; A represents the tree age; SA represents the age of each forest stand. The random parameter (ε) follows a normal distribution, representing the random effect of transects. Statistical analysis was conducted in R software environment (R 3.3.2) using "lme4" package (Bates et al., 2015). Variance inflation factors (VIFs) were also calculated to detect multicollinearity among different predictors (Belsley et al., 1980). Results showed that VIFs were lower than 2, which were lower than the accepted value of 4 (O'Brien, 2007). Nakagawa and Schielzeth (2013) reported a marginal R^2 (only fixed effects) and a conditional R^2 (both fixed and random effects) to provide the absolute values for the goodness of fit of LMMs. In this study, we also calculated them to represent the goodness of fit of the LMMs. In addition, analysis of variance decomposition was performed to quantify how much variance in the predicted square root of tree growth could be attributed to different fixed effect predictors. Decomposition of total variance was conducted by averaging sequential sum of squares over all orderings of the different variables, while this analysis was carried out using the "relaimpo" package in R environment (Gromping, 2006).

Table 1
Statistics of the linear mixed models over the 10, 20, and 30 years intervals for tree growth of trembling aspen and white spruce when using different competition indices including stand density index (SDI), sum of basal area (BA), sum of diameter at breast height (SDBH), and stem density (N), as well as similar indices for trees thicker than each subject (BAGR, SDBHGR, and NGR) as the predictor. Marginal R^2 represents contribution of fixed effect alone, while conditional R^2 represents contribution of both fixed and random effects. Bold words represent the highest R^2 for each species, and corresponding competition index will be used for following statistical analysis.

Time interval	Competition indices	Trembling aspen		White spruce	
		Marginal R^2	Conditional R^2	Marginal R^2	Conditional R^2
10	BA	0.417	0.490	0.469	0.614
	SDBH	0.408	0.485	0.476	0.610
	N	0.402	0.481	0.478	0.601
	BAGR	**0.567**	**0.741**	**0.484**	**0.611**
	SDBHGR	0.554	0.684	0.479	0.610
	NGR	0.533	0.624	0.475	0.606
	SDI	0.414	0.491	0.477	0.615
20	BA	0.457	0.538	0.542	0.648
	SDBH	0.440	0.535	0.533	0.649
	N	0.434	0.531	0.529	0.644
	BAGR	**0.595**	**0.774**	**0.550**	**0.651**
	SDBHGR	0.589	0.723	0.538	0.648
	NGR	0.568	0.665	0.532	0.647
	SDI	0.447	0.538	0.527	0.648
30	BA	0.453	0.512	0.563	0.642
	SDBH	0.436	0.510	0.562	0.657
	N	0.431	0.511	0.548	0.652
	BAGR	0.595	0.774	**0.569**	**0.655**
	SDBHGR	**0.597**	**0.716**	0.554	0.651
	NGR	0.576	0.650	0.552	0.653
	SDI	0.449	0.513	0.542	0.652

3. Results

Annual temperature and precipitation were simultaneously used as climatic indices for the whole statistical analysis. For the first analytical step, different competition indices were used separately in model (2) for different time intervals and tree species. The highest variance explanation of growth of trembling aspen and white spruce appeared when BAGR or SDBHGR was used as competition indices (Table 1). Therefore, competition indices with bold words in Table 1 will be selected out for following statistical analysis to compare effects of climate, competition indices, tree age and size on tree growth. Variance explanation varied with time intervals, while marginal R^2 ranged from 0.567 to 0.597 and from 0.484 to 0.569 for trembling aspen and white spruce, respectively. The values of R^2 showed a rising trend from 10 years to 30 years intervals, regardless of tree species.

Effects of competition indices on tree growth were more significant compared to climatic indices, especially for growth of trembling aspen (Fig. 3). Variance explanations (Adjusted R^2) of competition indices to trembling aspen growth were 0.302, 0.324, and 0.289 for 10, 20, and 30 years intervals, respectively. Variance explanations of competition indices to white spruce growth were 0.115, 0.143, and 0.169 for 10, 20, and 30 years intervals, respectively. Effects of climatic indices on tree growth was significant (positive relationship) for 30 years interval ($p < 0.05$), while it was insignificant for growth of 10 years interval, regardless of tree species. Tree growth of both species was positively affected by tree size (DBH), regardless of time intervals ($p < 0.05$). Variance explanations of tree size to trembling aspen growth were 0.153, 0.183, and 0.206 for 10, 20, and 30 years intervals, respectively. Variance explanations of tree size to white spruce growth were 0.179, 0.206, and 0.184 for 10, 20, and 30 years intervals, respectively. Effect of stand age on the white spruce growth was significant ($p < 0.05$), while the effect of stand age on trembling aspen growth was insignificant. Tree age was also an important factor for growth of white spruce, but not for growth of trembling aspen. Variance explanations of tree age to white spruce growth were 0.101, 0.095, and 0.082 for 10, 20, and 30 years intervals, respectively. Growth of trembling aspen was primarily affected by competition, followed by tree size. For white spruce, the growth was primarily influenced by tree size, followed by competition and tree age.

For trembling aspen, effect of CI_c on growth was more significant than that of CI_d, and both CI_d and CI_c negatively affected tree growth (Fig. 3). Variance explanations of CI_d to trembling aspen growth were 0.063, 0.077, and 0.094 for 10, 20, and 30 years intervals, respectively. Variance explanations of CI_c to trembling aspen growth were 0.239, 0.247, and 0.195 for 10, 20, and 30 years intervals, respectively. For white spruce, effect of CI_c on growth was more important than that of CI_d. Growth of white spruce was negatively affected by CI_d, whereas effect of CI_c on tree growth was positive (Fig. 3). Variance explanations of CI_d to white spruce growth were 0.058, 0.063, and 0.074 for 10, 20, and 30 years intervals, respectively. Variance explanations of CI_c to trembling aspen growth were 0.057, 0.081, and 0.095 for 10, 20, and 30 years intervals, respectively. Effects of climatic indices on tree growth of 30 years intervals were significant for both trembling aspen and white spruce. For 30 years interval, temperature and precipitation both positively influenced tree growth of trembling aspen and white spruce. Variance explanations of temperature and precipitation to trembling aspen growth were respectively 0.032 and 0.043 for 30 years intervals. For white spruce, variance explanations of temperature and precipitation to growth of 30 years intervals were 0.037 and 0.016, respectively.

Positive relationships between tree growth rates and DBH were found significantly for both tree species, and adjusted R^2 ranged from 0.472 to 0.702 and from 0.604 to 0.881 for trembling aspen and white spruce, respectively, within different time intervals (Fig. S3, $p < 0.001$). For trembling aspen, slopes were 0.539 ± 0.027, 0.539 ± 0.021, and 0.484 ± 0.015 for 10, 20, and 30 years intervals, respectively. For white spruce, slopes were 0.545 ± 0.019, 0.529 ± 0.013, and 0.508 ± 0.008 for 10, 20, and 30 years intervals, respectively. In this study, stem density showed negative relationship with stand age (Fig. 4). On the other hand, a significantly positive relationship (slope: 171.357 ±

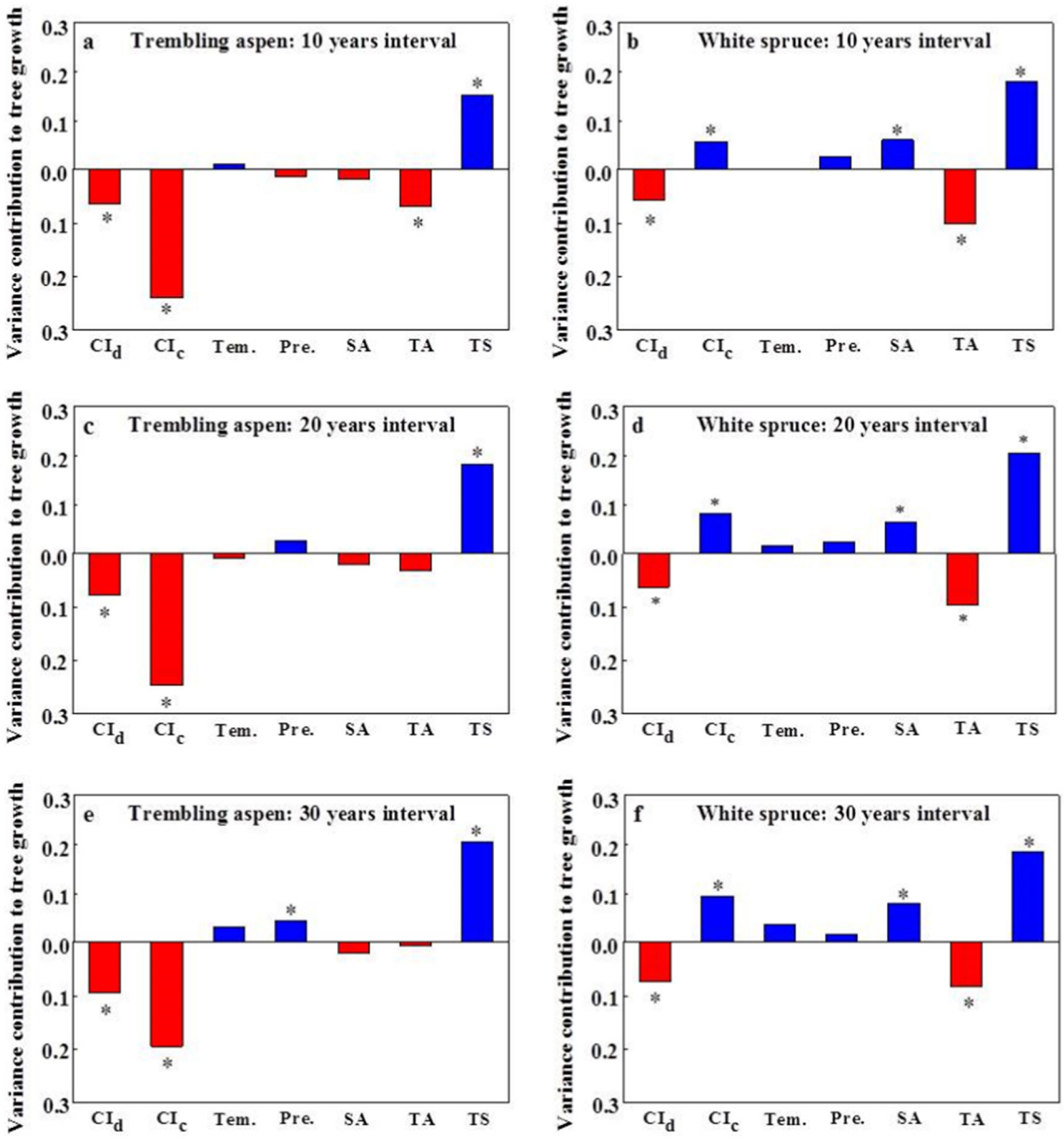

Fig. 3. Variance contribution of deciduous group competition index (CI_d), coniferous group competition index (CI_c), annual temperature (Tem.), precipitation (Pre.), stand age (SA), tree age (TA), and tree size (TS) to tree growth of trembling aspen (a, c, e) and white spruce (b, d, f) over different time intervals (10, 20, and 30 years). "Blue columns" and "red columns" represent positive and negative relationships between tree growth rates and different predictors, respectively. Asterisk means significant effect. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

30.024, adjusted $R^2 = 0.409$, $p < 0.01$) between stand stem density (stem ha^{-1}) and annual CMI (cm) was also found (Fig. S4).

4. Discussion

Results indicated that competition and tree size were two important driving factors influencing tree growth in boreal mixed forest of western Canada. In contrast, effects of climatic indices on individual tree growth were less important than those of competition and tree size for two dominant tree species of western Canadian boreal mixed forests. In western Canadian pure white spruce forest stands, it had been reported climatic changes could explain about 40% tree biomass increment (Hogg et al., 2017), which was inconsistent to our results. In Canadian mixed wood forests, it had been reported that climatic variables only captured ~40% variance in growth using tree ring chronologies (remove the competition, age, and size related variances in tree ring data) (Jiang et al., 2016), suggesting that there were other important factors influencing tree growth in mixed wood forests of this region.

In the western Canadian boreal mixed forests, trembling aspen is normally bigger in size and is available to compete for more resource than other species; therefore, it is initially expected that competition indices contributed less to growth of trembling aspen than other factors. However, for trembling aspen, it was surprising that competition indices showed more significant effects on tree growth than other factors in our study. White spruce, as a late successional and understory tree species, was commonly considered to be suffered more competition stress from trembling aspen (Cortini et al., 2012). However, white spruce growth was primarily affected by its size, followed by competition, suggesting a size-dependent mechanism controlling white spruce growth. Shade-tolerant species (such as white spruce) commonly obtain higher net carbon gain than shade-intolerant species (such as trembling aspen) under competition or environmental disturbance due to lower plant respiration rates of shade-tolerant species (Niinemets and

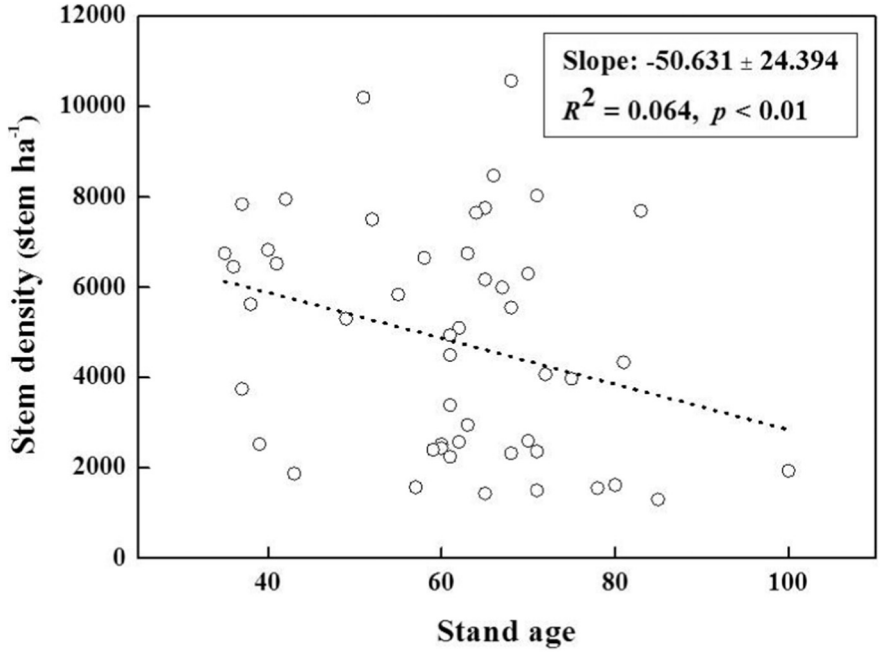

Fig. 4. Stem density (stem ha^{-1}) of different sampling transects in relation to stand age. The dot line was fitted trends using linear model with slope, R^2, and p values.

Valladares, 2006; Poorter et al., 2010); therefore, trembling aspen was more sensitive to water deficit and competition than white spruce.

This difference in competition effect between two species may be associated with the mechanisms of boreal forests succession and composition shift. Forest composition shift can both be affected by stand ageing process and climate change, while these two processes commonly operate in opposite direction to influence composition shift and contribute different amounts of variance to composition shift (Chen and Taylor, 2012; Searle and Chen, 2016). When forest tree growth is significantly influenced by competition, stand ageing process will show more significant effect on composition shift than climate change. Statistical results indicated that trembling aspen suffered more intense competition from neighbor trees, and then trembling aspen would be gradually replaced by late-successional species, suggesting that composition shift of boreal mixed forest was primarily controlled by stand ageing process. The relationship between white spruce growth and stand age was significantly positive ($p < 0.05$), suggesting that white spruce growth was greater in older forest stands. This result further demonstrated that the stand ageing process was tightly associated with forest composition shift in our study area.

It was surprising that tree growth was not primarily affected by climatic indices in our study, regardless of tree species. Previous studies illustrated that tree mortality significantly increased and forested area declined in some western Canadian boreal forests (Peng et al., 2011; Chang et al., 2014), while the water deficit was considered to be the dominant factor (Hogg et al., 2008; Michaelian et al., 2011). Western Canada is strongly controlled by continental climate, and thus water supply for tree growth is insufficient. Meanwhile, drought stress will be further intensified in this region under climate change. However, our results showed that effects of climatic indices were less important than those of other factors on individual tree growth rate, and climatic effect was even insignificant for 10 and 20 years intervals (Fig. 3). This phenomenon may be associated with the interaction among drought, stem density, and competition. A positive relationship was found between stem density and annual CMI in our study (Fig. S4, $R^2 = 0.409$, $p < 0.01$), suggesting that drought stress might significantly increase tree mortality and reduced live trees number in our study. Similar phenomenon had also been reported in previous studies (Peng et al., 2011; Chang et al., 2014). However, decline in stem density might also release competition stress of surviving trees. Tree ring samples were all collected from live trees, and our results suggested that warming and drought stress might have less effect on growth of surviving trees in the future. A large biomass loss from mortality was accompanied with a small tree growth increase in deciduous broadleaf forests (Chen and Luo, 2015). Hogg et al. (2002) also reported that tree growth increased under insect outbreaks, which was likely due to the resource release from tree mortality.

Growth of trembling aspen suffered more competition stress from coniferous group than that from deciduous group, indicating the strong effect of interspecific competition on trembling aspen growth. In contrast, relationship between growth of white spruce and competition of coniferous group was found to be positive for different time intervals (Fig. 3b, d, and f), suggesting an intraspecific mutualism mechanism within coniferous group. White spruce may affect the performance of neighboring trees either positively or negatively through interspecific and intraspecific interactions, and related mechanisms include soil nutrient availability improvement and belowground chemical interactions (Liu et al., 2010; McIntire and Fajardo, 2014). The association with neighboring spruce might improve soil microbial community by increasing arbuscular mycorrhizal fungi, and might induce the production of tree roots (Xia et al., 2016). Reduction of drought stress was another potential mechanism of intraspecific facilitation that influenced neighboring white spruce growth (Renard et al., 2016). Statistical analysis of relationship between growth rates and competition indices would overlap effects of both competition and mutualism on tree growth, while these two effects could not be separately quantified using model analysis. Our results demonstrated that, for white spruce growth, mutualism offset the competition within coniferous group. However, growth of trembling aspen was not only restricted by intraspecific competition, but also depressed by interspecific competition.

Gray and Hamann (2011) indicated that climate change would cause substantial reduction of white spruce in western Canada, suggesting that forest ecosystems in this region would no longer be suitable for white spruce growth. However, our results showed that white spruce growth was less affected by climatic indices, because the mutualism mechanism within coniferous group and decline in wood density released competition stress for surviving white spruce. In contrast, intensely intraspecific and interspecific competition might depress growth of trembling aspen, and cause potential decline of trembling aspen in western Canadian boreal mixed forests.

Besides climatic and competition indices, it had been reported that tree size and age governed response of tree growth to climate change (Martinez-Vilalta et al., 2012; Zhang et al., 2015). One previous study reported that effects of tree age and size on tree growth were more important than those of annual climatic variables (Foster et al., 2016). In our study, tree size was also a significantly important factor influencing tree growth, especially for white spruce. Significant effect of tree size on growth indicated a competition related mechanism, the "initial size advantage hypothesis", which stated that trees with a larger size were more competitive than their smaller cohorts (Larocque, 1998), and tree size could explain a larger portion of the variation in growth.

5. Conclusions

In boreal mixed forests of western Canada, it was demonstrated that effects of competition and tree size on tree growth were dependent on tree species, while climatic variables showed less important or insignificant effects. Growth of trembling aspen was negatively affected by inter- and intraspecific competition, while intraspecific competition showed positive effect on growth of white spruce. Growth of trembling aspen was primarily affected by exogenous factors (such as competition), while growth of white spruce was primarily dependent on endogenic factors (such as tree size), indicating a competition driven succession in the boreal mixed forests. Although increased tree mortality caused by severe drought stress have been reported in our study area, our results suggested that tree biomass loss under drought also release competition stress for surviving trees. In this way, climatic variables did not significantly affect growth of surviving trees, which reserved the potential of forest restoration after severe drought in this region. These findings might contribute to an improved prediction of forest development in western Canadian boreal mixed forests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.03.099.

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